

The University of Chicago

ECOLOGICAL ASPECTS OF TRANSPIRATION

A DISSERTATION SUBMITTED TO THE
FACULTY OF THE DIVISION OF THE BIO-
LOGICAL SCIENCES IN CANDIDACY FOR
THE DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF BOTANY

By
CHARLES WHITFIELD, JR.

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ECOLOGICAL ASPECTS OF TRANSPIRATION

I. PIKE'S PEAK REGION: CLIMATIC ASPECTS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 437

CHARLES J. WHITFIELD

(WITH EIGHT FIGURES)

Introduction

During the past three years, transpirational and instrumental studies have been conducted in the principal vegetational climaxes of the Pike's Peak region, Colorado, and Santa Barbara County, California. These regions are well suited for studies of this type because in each of them there are several climaxes in close proximity to one another. In the Pike's Peak region, in a distance a little more than seven miles by airline, six climaxes are represented (CLEMENTS 1). Since the chaparral and woodland climaxes are limited in extent, little or no experimental work was done in these two associations. The remaining four climaxes, plains, montane forest, subalpine forest, and alpine tundra, are the conspicuous ones of the region.

The plains, with *Bouteloua gracilis*, *Stipa comata*, and *Sporobolus cryptandrus* as the conspicuous dominants, are characterized by high temperatures, saturation deficit, evaporation, and wind; and by low relative humidity, holard, and rainfall. *Pseudostuga mucronata* and *Pinus ponderosa* are the important dominants of the montane zone, which is characterized by higher relative humidity, holard, and rainfall; and by lower temperatures, saturation deficit, evaporation, and wind. The dominants of the subalpine association are *Picea engelmanni* and *Pinus aristata*. This zone has higher relative humidity, rainfall, and wind than the montane zone, and lower temperatures and saturation deficit. The climax species of the alpine tundra are *Elyna bellardi* and *Carex rupestris*. Here are the highest relative humidity, holard, wind velocity, and rainfall, and the lowest temperatures and saturation deficit.

The ecology of this region has been discussed in two previous papers which deal with vegetational and instrumental aspects of the

different climaxes (7, 8). The objects of the present study are the measurement of the water loss in relation to the physical factors in as many climaxes as possible, and the establishment of correlations between factor and function. The materials for this paper have been drawn from the projects now being conducted in this region by the Carnegie Institution of Washington under the direction of Dr. F. E. CLEMENTS.

Methods

Transpiration of native and control plants (sunflower, corn, wheat) was measured in the different climaxes by means of the phytometer or gravimetric method; environmental data were obtained by using batteries of instruments. The historical aspects of the phytometer method have been discussed by CLEMENTS and GOLDSMITH (2) and MAXIMOV (5). In this paper the term phytometer is employed to designate any plant or group of plants used for functional purposes, and implies the use of the gravimetric method (2). The methods used here, although they agree in principle, differ in detail from those employed by BRIGGS and SHANTZ, WEAVER, and CLEMENTS and GOLDSMITH.

EQUIPMENT.—Unless otherwise stated, cylinders 9 inches tall by 5.5 inches wide were used. These were made of 28-gauge galvanized iron, and waterproofed by soldering the bottoms and sides. The containers were equipped with slightly tapering lids with a 2-inch opening. Both the lid and the cylinder were provided with a 0.75 inch crimp to permit a closer fit, and the lid was further sealed by plumber's tape or an equal mixture of beeswax and paraffin. Near the bottom of each container a bicycle valve-stem, with the core removed, was inserted for aeration. For watering purposes a glass tube, 0.5 inch wide and approximately 11 inches long, was inserted in each container through the opening of the lid. A rubber stopper was put in the glass tube to prevent evaporation. In all cases, a half-inch of coarse gravel was placed in the bottom of the container, level with the lower end of the glass tube. With the water equally distributed in the gravel, movement into the soil took place more evenly.

PLANTS, STANDARD AND NATIVE.—When sunflowers, wheat, or corn, the controls or standards, were used, the following procedure was employed. In order to have enough material for selective pur-

poses, approximately twice as many plants were grown as were needed for the various stations. First the gravel and the glass tubes were placed in the desired number of containers. Next the latter were filled with soil previously screened and of good tilth. In order to pack the soil, the cans were lifted approximately 6 inches from the ground and allowed to fall several times during the filling. When the containers were full, with lids sealed in place, the seeds were planted just below the soil surface. They were then watered and covered to prevent drying, and allowed to develop to the four-leaf stage.

After the plants had reached this stage they were watered, sealed, aerated, and standardized. By means of a burette, the same amount of water was added for each of the plants. Each container was aerated by attaching to it a water aspirator, or suction pump, fastened to an ordinary garden hose. Gas analyses showed that aerating each container for 4 minutes was sufficient. The results of a 4-minute test were: before aerating, oxygen, 18.71 per cent; carbon dioxide, 2.09 per cent; after aerating, oxygen, 20.95 per cent; carbon dioxide, 0.48 per cent.

For standardization purposes, a temporary seal of very fine sand or a light coat of paraffin was sufficient to prevent evaporation. Leaf areas were determined, the plants were weighed, and then placed in a greenhouse on a revolving table which rotated once every 10 minutes. After 2 days the plants were remeasured, reweighed, and classified according to their losses. Plants which transpired the same amount on the revolving table were distributed among the various climaxes or stations, the same number of plants being sent to each station. In this way not only the individual plants but also the batteries at each station were equivalent.

After standardization, the plants were brought to their original weight by watering through the tubes. They were then aerated and permanently sealed. In many cases assistants were located at each station to protect the phytometers from rain, so that the permanent sealing was chiefly a matter of prevention of evaporation. When the plants were left unprotected, however, it was necessary to seal them, not only to prevent evaporation but also to prevent rain from entering. After a number of years of experimentation in different habitats, it became evident that each climax required a particular seal.

At Santa Barbara, where the experiments can be conducted between rains, all that is necessary is a fine sand over the soil, with a piece of oilcloth over the top of the can to prevent the wind from blowing the sand. On the Colorado plains, with both high temperatures and rains, non-absorbent cotton and tinfoil in the form of miniature umbrellas were placed around the stem. The cotton was used to permit expansion by growth, as well as to prevent the warm paraffin from coming in contact with the stem. The tinfoil umbrellas helped deflect the rain which might otherwise run down the stems of the plants. The soil was covered with a mixture of equal parts of beeswax and paraffin. The gap left between the seal and the container was filled in most cases by melting the outer edge of the former with a hot rod, and in other cases by plasticine. This seal was further protected by rubber sheeting or oilcloth.

Finally the phytometers were again measured and weighed, and then placed in typical habitats. A typical battery for each station consisted of eight to ten plants. The plants were taken to the various habitats by Cog train and automobile in Colorado, and by automobile in California. In all cases, unless otherwise mentioned, the containers were sunk in the ground so that the plants would be at the same level as the native vegetation; this had the further advantage of keeping the soil temperature of the phytometers approximately the same as that of the surrounding habitat. The average length of time for most of the series was 2-4 days. The plants were remeasured and reweighed at the end of the experiment, and returned to the laboratory for restandardization. Sometimes, if the plants were in good condition, the experiments were continued for another period of 2-4 days.

Losses were figured on the basis of either leaf area or standardization. In figuring leaf areas of sunflowers, the method developed by CLEMENTS and GOLDSMITH (2) was used. Briefly, the leaf area of sunflower leaves in square centimeters was found by multiplying the product of the extreme dimensions measured in millimeters by the factor 0.013. For wheat and corn, the length and width of each blade were measured. When native plants were used, this procedure was followed with the exception that the containers were filled with native soil, and the transplants allowed time for readjustment.

SHORT-PERIOD PHYTOMETERS.—In all the experiments, short-period phytometers were employed. Small cylinders of the size already mentioned are more easily distributed, weighed, and protected in the field than are those of larger dimensions. With small containers it is also possible to have a greater number of plants in each habitat, which is a very desirable factor. By this method the initial responses of the phytometers to the various habitats are measured. Moreover, when plants like sunflowers are used, they are not left in small containers long enough to cause unnatural root development, which influences the functional responses.

The results of experiments conducted with short-period phytometers and potometers at different stations showed that the functional and stomatal responses of the potometers did not coincide with those of the phytometers. These conclusions led to the exclusive use of short-period phytometers in this work.

Results

In order to measure the environmental factors, batteries of instruments were placed with the phytometers in the various habitats. The battery, together with the simple instruments, consisted of a hygrothermograph, cog psychrometer, thermometer, evaporimeter, black and white atmometers, anemometer, and rain-gauge. In Colorado, soil thermographs were also used.

FIRST SERIES.—Two species, *Helianthus annuus* and *Triticum sativum*, were used as phytometers in the initial series. Since a revolving table was not available in this case, the plants were placed in a greenhouse and each phytometer shifted every hour during the day. General sky conditions during the experiment were similar at the three stations, with the mornings clear and the late afternoons usually cloudy. A slight rain was reported throughout in the afternoon of Friday, June 28.

The average leaf area of the ten plants of *Triticum sativum* was 24.85 sq. cm. at the plains station, 24.25 sq. cm. at the montane station, and 26.57 at the alpine station. The average leaf area of *Helianthus annuus* at the three stations was 75.08, 72.43, and 68.48 sq. cm. respectively.

The factor data were secured and computed according to methods

described in a previous paper (7). The experiment was started at 6 P.M., June 25, and closed at 6 P.M., June 28, 1929. Readings were made at 6 P.M. and 6 A.M. throughout the series. The day and night readings thus secured were averaged and added to get the daily averages shown in figure 1. All are daily averages except the relative humidity, which is for the day only.

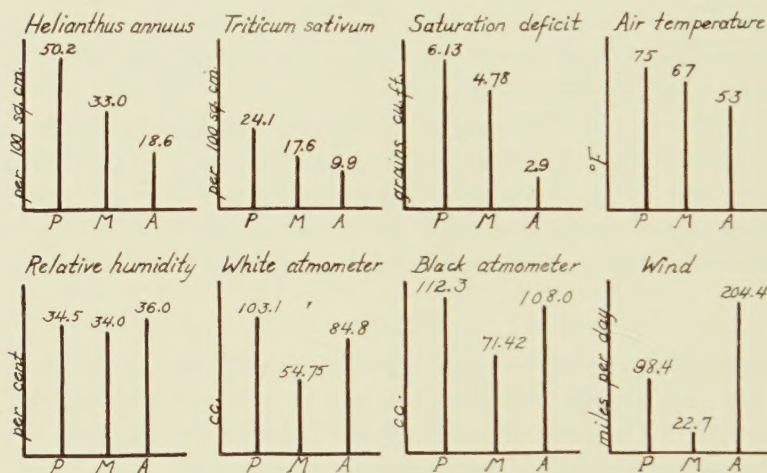


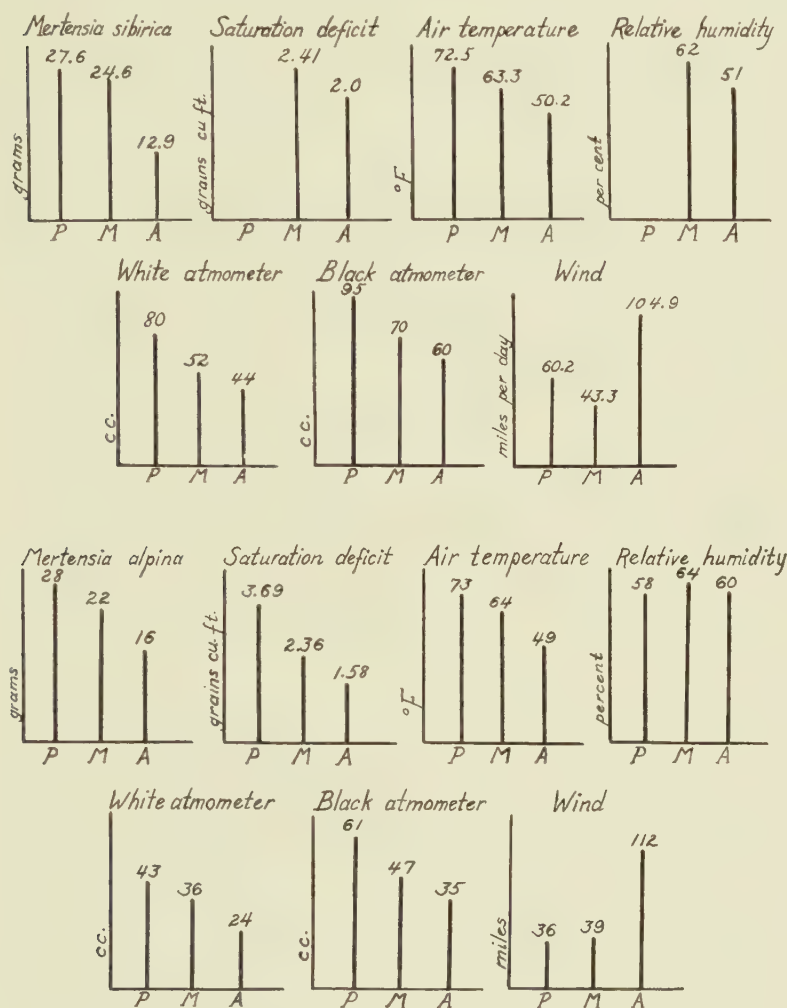
FIG. 1.—First series, June 25–28, 1929: P, plains, M, montane; A, alpine

SECOND SERIES.—In this experiment specimens of a native species, *Mertensia sibirica*, were used as phytometers. This species was chosen because of its value in the transplant experiments, large leaf surface, and wide distribution. During the series no rain fell at the plains, 0.3 inch fell at the montane, and 0.07 inch fell at the alpine station. The plants in all cases were protected from rain. Saturation deficits based on readings of air temperatures and relative humidities taken at 6 A.M., 12 noon, and 4:30 P.M. on July 5 were: plains, 8.47; montane, 4.34; and alpine, 2.42 grains per cu. ft.

The series was conducted during the period July 3–7, 1930. Readings were made at 6 A.M. and 6 P.M. (fig. 2).

THIRD SERIES.—*Mertensia alpina*, an alpine species, was employed in this series. A smaller container, 5 inches tall and 5.5 inches wide, was used. The series was conducted at the three climatic stations

during the period July 9-12, 1930. Weighings were made at 6 P.M. (fig. 3).



FIGS. 2, 3.—Fig. 2 (above), second series, July 3-7, 1930; daily averages. Fig. 3 (below), third series, July 9-12, 1930; daily averages.

FOURTH SERIES.—Three species, *Helianthus annuus*, *Mertensia sibirica*, and *M. alpina* were used as phytometers at six stations: plains, woodland, montane, subalpine, alpine, and summit. *Helian-*

thus was distributed to all stations; *Mertensia sibirica* to the plains, montane, subalpine, and alpine stations; and *M. alpina* only to the

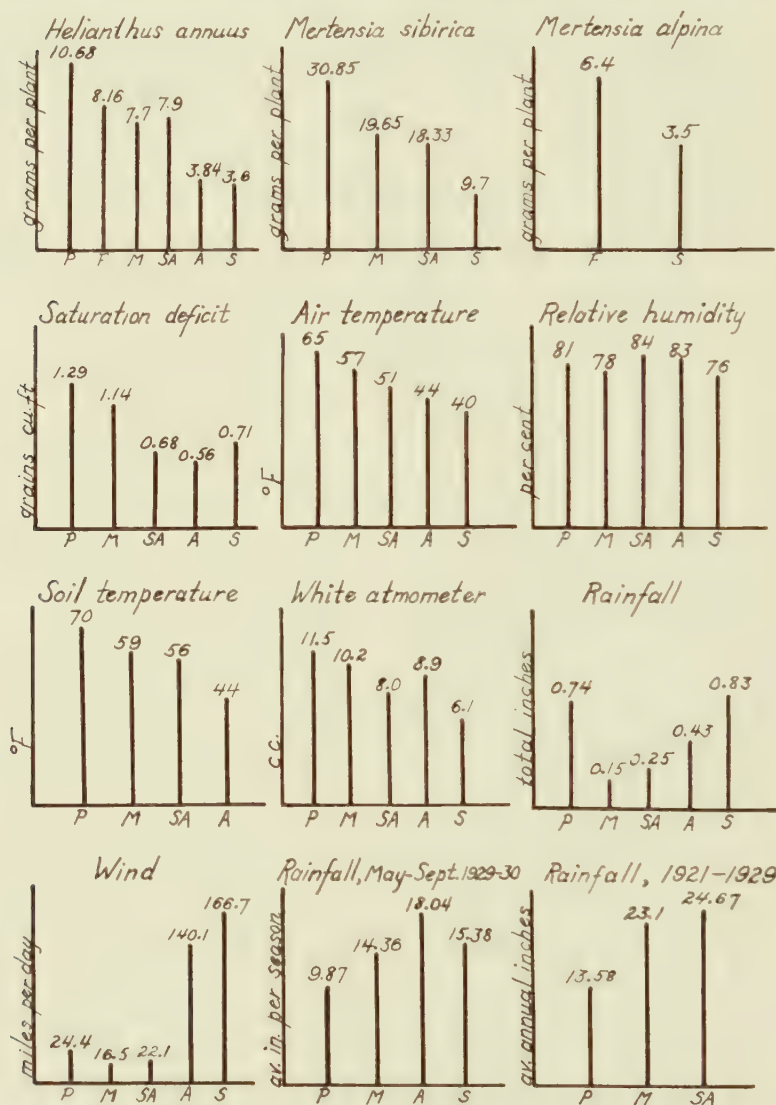


FIG. 4.—Fourth series, July 28-31, 1930: P, plains; F, foothills; M, montane; S, subalpine; A, alpine; S, summit.

foothills and summit. Weather conditions during this experiment were adverse. Rain was reported at all stations, but it was particu-

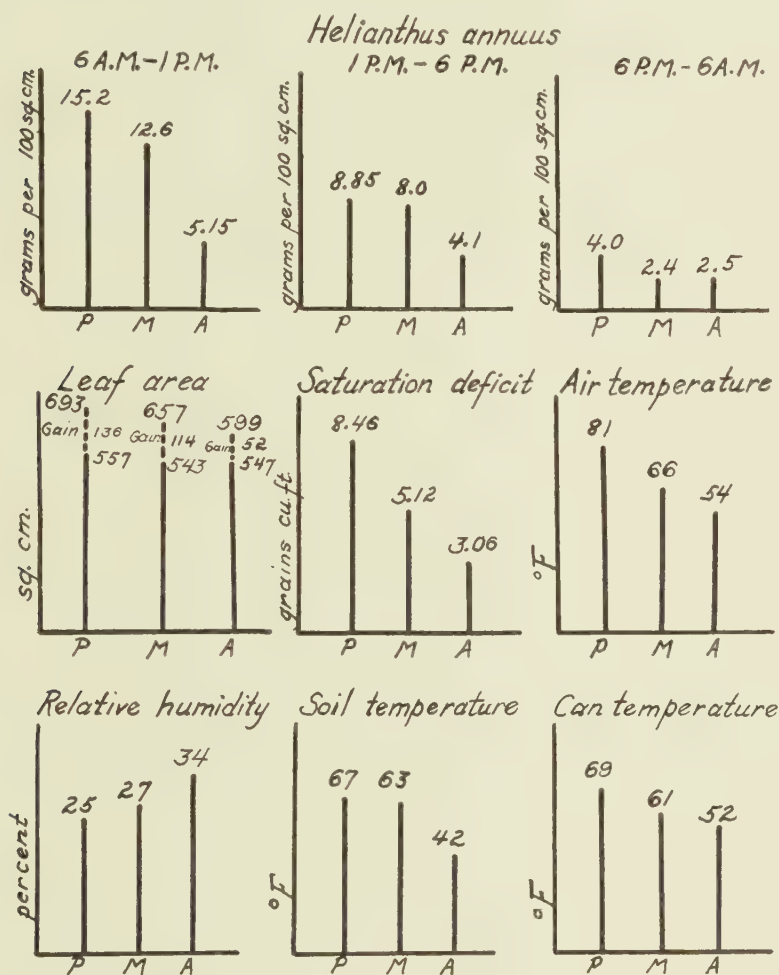


FIG. 5.—Fifth series, July 18-20, 1931

larly heavy at the plains and summit. In general, however, the climatic environmental relationships of the various stations were maintained.

The experiment was conducted from July 28 to 31, 1930. Readings were made at 5 P.M. daily (fig. 4).

FIFTH SERIES.—*Helianthus annuus* was used in this series. The phytometers were placed in lath-houses at each station. During the

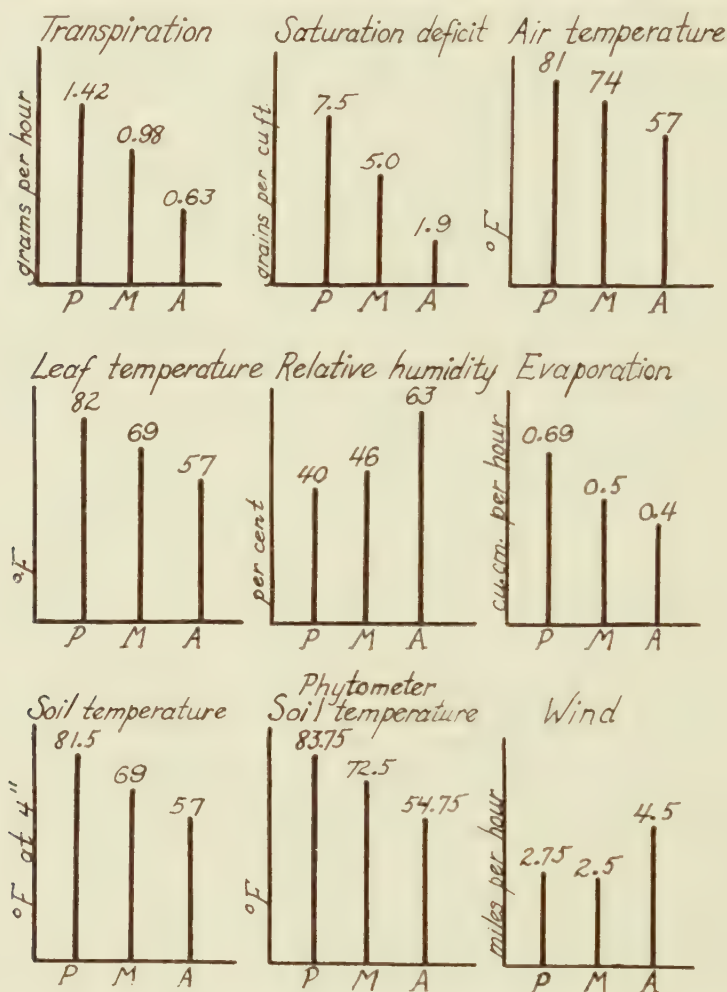


FIG. 6.—Sixth series, July 27-30, 1931 (see table I)

experiment light readings were taken in the lath-houses. Averages of three readings, made at 9 A.M., 12 noon, and 3 P.M., were as follows: plains, 19.5; montane, 18.4; and alpine, 17.2 per cent. Hand photometers were used to measure the light.

TABLE I
TRANSPIRATIONAL AND INSTRUMENTAL DATA, SIXTH SERIES (cf. FIGURE 6)

		TIME																		
		7/27 6 P.M.	7/28 6 A.M.	8 A.M.	10 A.M.	12 N.	2 P.M.	4 P.M.	6 P.M.	8 P.M.	12 M.T.	7/29 4 A.M.	6 A.M.	8 A.M.	10 A.M.	12 N.	2 P.M.	4 P.M.	6 P.M.	7/30 6 A.M.
Transpiration per 100 sq. cm.																				
P.		1.8	3.7	5.9	7.6	5.8	5.3	2.6	0.8	0.7	0.4	1.0	3.1	5.3	6.4	7.4	8.3	4.9	2.8	
M.		1.8	3.6	5.5	7.4	4.3	1.5	1.8	0.4	0.1	0.1	0.2	2.9	4.9	6.1	6.9	6.2	3.6	1.9	
A.		1.8	2.0	3.7	4.6	1.9	1.2	1.2	0.6	0.5	0.6	0.3	1.5	3.0	4.0	4.1	3.4	2.2	1.3	
Air temperature																				
P.		80	86	92	94	87	80	76	71	63	60	68	74	80	90	85	91	85	61	
M.		70	65	85	88	78	70	68	62	50	50	57	70	75	75	79	77	69	60	
A.		59	53	67	68	58	58	55	51	46	46	46	53	60	61	61	60	50	47	
Leaf temperature																				
P.		88	88	90	92	82	83	86	72	66	63	70	72	80	86	80	88	85	81	
M.		68	61	75	82	72	64	61	55	52	52	54	60	76	73	79	77	59	50	
A.		58	52	64	62	57	50	53	52	46		48	58	60	60	59	57	55	46	
Relative humidity																				
P.		30	57	33	27	32	38	49	52	64	67	63	60	54	38	27	15	17	64	
M.		49	52	41	31	28	35	52	54	54	63	61	55	53	43	33	28	43	57	
A.		73	83	70	62	74	69	59	73	87	75	81	65	56	54	52	48	64	81	
Saturation deficit																				
P.		7.65	2.92	8.53	11.45	9.20	6.78	4.92	3.06	2.29	1.00	2.77	3.63	5.03	8.90	9.30	12.05	10.57	2.14	
M.		4.07	3.17	6.25	8.52	6.08	3.83	3.44	2.82	2.21	1.86	2.02	3.59	4.40	5.34	7.10	7.88	4.11	2.47	
A.		1.30	0.74	1.61	2.84	1.30	1.61	2.06	1.27	0.46	0.89	0.70	1.58	2.30	2.73	3.15	2.89	1.81	0.70	
Soil temperature																				
P.		91	77	76	80	83	85	85	83	78	75	74	74	78	84	90	88	86	74	
M.		73	66	65	66	69	72	73	72	67	65	64	63	65	68	72	75	75	65	
A.		60	51	60	53	60	62	59	56	53	50	49	49	52	58	64	66	66	50	
Phytometer soil temperature																				
P.		94	79	76	80	87	90	87	84	78	75	73	73	77	83	89	93	94	73	
M.		80	66	65	70	75	77	74	71	65	63	61	62	67	74	80	81	82	64	
A.		77	51	52	54	59	60	58	56	53	49	48	49	53	57	53	60	64	51	
Piché evaporimeter																				
P.		3.58	1.67	3.60	4.0	2.3	1.80	1.0	0.8	1.4	0.6	0.4	1.7	2.6	1.62	2.68	3.3	2.9	3.3	
M.		3.0	1.05	2.05	2.9	1.9	0.8	0.8	0.5	1.2	1.1	0.6	0.8	1.2	1.0	2.80	2.1	1.7	3.3	
A.		2.05	1.25	1.50	2.2	1.14	0.5	0.75	0.75	1.0	1.1	0.5	0.8	1.2	1.8	1.86	1.6	1.2	2.1	
Anemometer																				
P.		16.2	3.59	16.2	11.1	6.2	4.4	0.71	2.7	13.7	1.9	2.4	22.2	20.4	9.5	6.9	9.2	7.6	7.9	
M.		26.9	3.1	4.5	9.6	5.8	5.7	4.2	4.7	8.9	10.2	6.0	8.9	5.0	8.7	6.6	6.6	4.9	27.0	
A.		40.4	12.8	11.6	14.9	13.3	8.8	7.5	17.9	5.4	15.8	9.2	8.1	0.8	10.8	11.9	11.7	7.3	41.6	

The series was started at 1 P.M., June 18, and closed at 1 P.M., June 20, 1931. Weighings were made at 6 A.M., 1 P.M., and 6 P.M. (fig. 5).

SIXTH SERIES.—Plants of *Helianthus annuus* were used as phytometers for the series conducted at the plains, montane, and alpine stations (fig. 6 and table I). General sky conditions at the three stations were similar, all three having approximately the same amount of sunshine and cloudiness. The first day was clear until noon and cloudy all afternoon. During the second day weather conditions were more or less intermittent up to three o'clock and then clear. Hand-photometer readings taken every hour at the three stations

TABLE II

STOMATAL RELATIONS OF PHYTOMETERS, SIXTH SERIES. KEY: o=closed;
 $\frac{1}{2}$ =nearly closed; 1 = $\frac{1}{2}$ open; 2 = $\frac{2}{3}$ open; 3 = $\frac{3}{4}$ or more open

	TIME																			
	6	8	10	12	2	4	6	8	12	4	6	8	10	12	2	4	6	6		
	A.M.	A.M.	A.M.	M.	P.M.	P.M.	P.M.	P.M.	MT.	A.M.	A.M.	A.M.	A.M.	M.	P.M.	P.M.	P.M.	A.M.		
Plains.....	o	1-o	1-o	1	2	2-3	2	1-2	1	2	1-2	2	3	1	3	1	1	1	1	1
Montane....	1-2	2-3	1-2	2	1	o-1	$\frac{1}{2}$	o- $\frac{1}{2}$	o	o	o- $\frac{1}{2}$	1	1	o- $\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$	o-1	1
Alpine.....	1-2	2	2	2	1-2	o-1	$\frac{1}{2}$	1-2	o-1	2	o- $\frac{1}{2}$	1	1-2	1-2	1	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$

showed the following averages: plains 62.3, montane 46.9, and alpine 52.7 per cent. Averaged evaporimeter readings made simultaneously at the three stations were: plains 6.55, montane 4.53, and alpine 3.27 gr. per 100 cm.² per hour. These results are in general accord with those secured by the Piché evaporimeter. Leaf areas were taken at the beginning and end of the experiment. Greatest growth took place at the plains, with the least at the alpine station, the increases being 42, 38, and 32 sq. cm. per plant respectively.

The condition of the stomata with reference to the degree of opening was also considered. Stomatal strips were made and examined from plants used only for this purpose.

The stomatal relations are shown in table II.

The experiment was started July 27, 1931, at 6 P.M. and closed at 6 A.M., July 30. Weighings and stomatal strippings were made at 2-hour intervals from 6 A.M. to 6 P.M., and at 8 P.M., 12 midnight, and

4 A.M. during the night of July 28-29. Instrumental records were made hourly between 6 A.M. and 6 P.M., and at 8 P.M., 12 midnight, and 4 A.M. during the night of July 28-29.

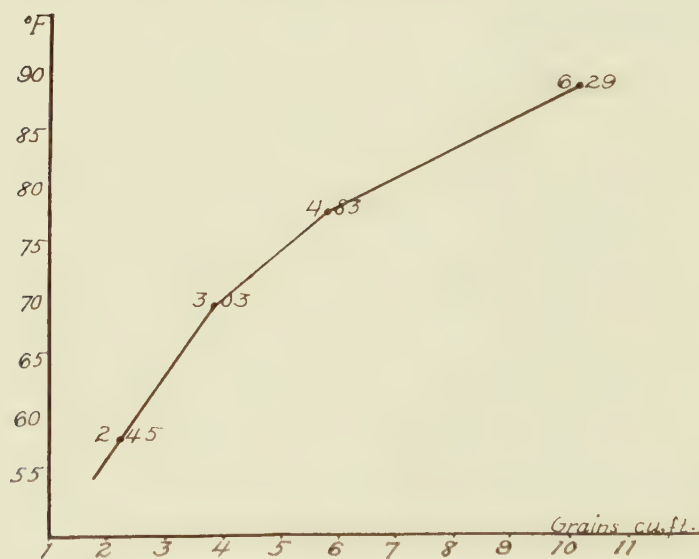
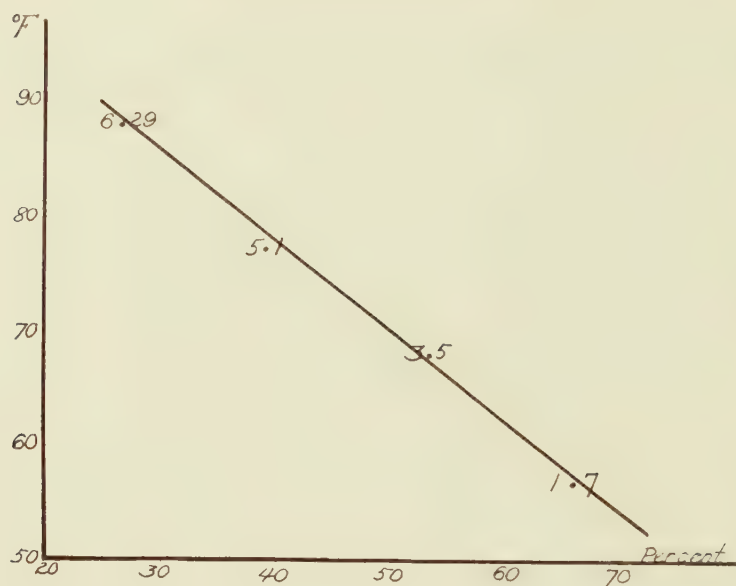
Discussion

Helianthus annuus, *Mertensia sibirica*, *M. alpina*, *Triticum sativum*, and *Chamaenerion angustifolium* were used as phytometers in the various climatic formations of the Pike's Peak region, Colorado. Eight different climatic series were conducted to record the transpiration and the climatic conditions, and to study the relations between them in the principal formations.

In all cases transpiration decreased with increased altitude. This was true for all species used in the different series. Of the various climatic conditions measured, evaporation, soil and air temperatures, and saturation deficits decreased with increased altitude. On the other hand, the approximate values of the maximum intensity of radiant energy on a clear day were 1.48, 1.58, and 1.64 cal. per cm.² per min. for plains, montane, and alpine respectively, showing increased values with increased altitude. However, the total energy over a season might reverse these readings because of the more cloudy conditions in the alpine region. No data are at present available on this problem. Relative humidities, rainfall, and hoard are usually greater at the higher elevations. Wind is constantly highest in the alpine region, with the plains next, and the montane zone ordinarily the lowest.

Few exact studies have been made in the field of the relationship between transpiration and the main climatic factors. In the present studies, close correlations have been secured with isolated factors as well as combinations of some of the principal climatic factors.

A close relationship exists between transpiration, air temperature, and relative humidity, and between transpiration and a combination of these two factors (fig. 7). The average air temperature, relative humidities, and transpiration of the natural groups approximates a straight line. This relationship is strengthened by the fact that the average air temperatures, relative humidities, and transpiration at the main climatic stations indicate a straight line. While the results approximate a straight line between transpiration, air temperature,



FIGS. 7, 8.—Fig. 7 (above), temperature-relative humidity-transpiration. Fig. 8 (below), temperature-saturation deficit-transpiration.

and relative humidity, such a correlation does not exist between transpiration, saturation deficit (fig. 8), and evaporation. The transpirational points which fall naturally on an approximately straight line with air temperature and relative humidity do not do so with saturation deficit and evaporation. These results show that the two curves of transpiration and saturation deficit do not run parallel. In addition, the mathematical ratios of transpiration and saturation deficit are irregular. The fact that the points do not approximate a straight line, as well as the irregularity of the ratios, indicates that saturation deficit does not bear so close a relation to transpiration as do air temperature and relative humidity.

In comparing transpiration and evaporation per 100 cm.² per hour, the water loss of the improved evaporimeter (6) was approximately five times that of the phytometers. The ratios between the two were regular for the plains and alpine stations, but were irregular for the montane.

Observations made on sky conditions during the various series indicate a relation between transpiration and radiant energy. During the first day of the sixth series the sky was clear until noon and cloudy in the afternoon; during the second day weather conditions were more or less variable up to 3 o'clock and then clear until sunset. Transpiration showed an increase until noon of the first day and then decreased; while during the second day transpiration rose in steps, reaching the maximum about 3 P.M., then dropping with the other factors.

The results of growth measurements made during the various series show that the greatest increase took place at the plains station, the smallest at the alpine station. The ratios between transpiration and growth at the plains, montane, and alpine stations were 0.207, 0.202, and 0.226 respectively, indicating a close relationship between these two functions.

These results indicate relations between factor, function, and vegetation. Climatically the conditions at the plains station are the best for growth, but due to low soil moistures the vegetation is mixed prairie. The montane zone, although having a shorter growing season than the plains, is not limited by any other climatic or edaphic factor. In consequence the climatic vegetation is forest rather than

grassland. The alpine tundra shows the least xeric tendencies of all by having low transpiration, evaporation, and saturation deficits, and high humidities and holard. In spite of these mesophytic characteristics, however, the alpine vegetation is composed of dwarf grasses and sedges. This is probably due to the reduced air pressure which expresses itself most strongly in the low air and soil temperatures. The temperatures often become so low during the short growing season that the availability of water is limited. It is in such times of stress that the xeromorphic structures of the alpine plants become useful by limiting to a great extent the water loss.

Summary

1. A comparison of the plains, montane, and alpine climates of the Pike's Peak region showed that: (a) air and soil temperatures, saturation deficit, and evaporation decrease with increased altitude; (b) radiant energy, relative humidities, rainfall, and holard are usually greater at higher elevations; (c) wind movement is constantly highest in the alpine region, with the plains next, and the montane zone ordinarily the lowest.

2. A comparison of the functional responses of plants in these three climates showed: (a) a decrease of transpiration with increased altitude; (b) a decrease of growth rate with increased altitude.

3. The transpiration curve showed a closer correlation with the air temperature and the relative humidity curves than with any of the other factors measured.

4. Evaporation was approximately five times as great as transpiration in the three regions.

5. Vegetation does not respond to any one factor, but rather to all of the climatic conditions.

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